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Minireview

Disease will limit future food supply from the global crustacean fishery and aquaculture sectors

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ABSTRACT

Seafood is a highly traded food commodity. Farmed and captured crustaceans contribute a significant proportion with annual production exceeding 10 M metric tonnes with first sale value of \$40bn. The sector is dominated by farmed tropical marine shrimp, the fastest growing sector of the global aquaculture industry. It is significant in supporting rural livelihoods and alleviating poverty in producing nations within Asia and Latin America while forming an increasing contribution to aquatic food supply in more developed countries. Nations with marine borders often also support important marine fisheries for crustaceans that are regionally traded as live animals and commodity products. A general separation of net producing and net consuming nations for crustacean seafood has created a truly globalised food industry. Projections for increasing global demand for seafood in the face of level or declining fisheries requires continued expansion and intensification of aquaculture while ensuring best utilisation of captured stocks. Furthermore, continued pressure from consuming nations to ensure safe products for human consumption are being augmented by additional legislative requirements for animals (and their products) to be of low disease status. As a consequence, increasing emphasis is being placed on enforcement of regulations and better governance of the sector; currently this is a challenge in light of a fragmented industry and less stringent regulations associated with animal disease within producer nations. Current estimates predict that up to 40% of tropical shrimp production (>\$3bn) is lost annually, mainly due to viral pathogens for which standard preventative measures (e.g. such as vaccination) are not feasible. In light of this problem, new approaches are urgently required to enhance yield by improving broodstock and larval sourcing, promoting best management practices by farmer outreach and supporting cutting-edge research that aims to harness the natural abilities of invertebrates to mitigate assault from pathogens (e.g. the use of RNA interference therapeutics). In terms of fisheries losses associated with disease, key issues are centred on mortality and quality degradation in the post-capture phase, largely due to poor grading and handling by fishers and the industry chain. Occurrence of disease in wild crustaceans is also widely reported, with some indications that climatic changes may be increasing susceptibility to important pathogens (e.g. the parasite *Hematodinium*). However, despite improvements in field and laboratory diagnostics, defining population-level effects of disease in these fisheries remains elusive. Coordination of disease specialists with fisheries scientists will be required to understand current and future impacts of existing and emergent diseases on wild stocks. Overall, the increasing demand for crustacean seafood in light of these

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issues signals a clear warning for the future sustainability of this global industry. The linking together of global experts in the culture, capture and trading of crustaceans with pathologists, epidemiologists, ecologists, therapeutics specialists and policy makers in the field of food security will allow these issues to be better identified and addressed.

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1. Food security and globalisation in context

Global population projections predict expansion of the human population from the current estimate of 7bn to between 8.8 and 9.1bn by 2050 (Fischer et al., 2009; Anderson, 2010). However, the proportional change in different global regions is not equal, with projections for so-called High-Income Countries (HICs) such as the USA and countries of Europe remaining almost static against significant proportional increases in South and East Asia, the Middle East, North Africa and sub-Saharan Africa (Fischer et al., 2009; Anderson, 2010). In the context of food consumption, it is clear that not only will this increase require significantly elevated overall food production but changes in consumption patterns (e.g. the shift from grains and other staples towards livestock) will accompany the expanding middle-income sector within these growing populations (Anderson, 2010).

In the three decades between 1970 and 2000, significant increases in global food consumption per capita have occurred, rising by almost 400 kcal per person per day over the period. This has resulted in reductions in under-nutrition and food poverty globally, though this trend has not been observed in some regions (e.g. sub-Saharan Africa) (Kearney, 2010). Interestingly, not only has calorie consumption changed but diet composition has also shifted in several regions; for example in China, the increased available consumption of vegetable oils (680%), meat (349%) and sugar (305%) has accompanied a decline in consumption of pulses, roots and tubers over the period 1963–2003 (Kearney, 2010). It is noted that these large scale shifts in consumption pattern occur in two distinct phases, the first involving an ‘expansion’ in calorie intake (i.e. from cheaper food stuffs of vegetable origin), and the second involving ‘substitution’ of these carbohydrate-rich staples with vegetable oils, animal products (meat and dairy foods) and sugar

(Kearney, 2010). It is generally accepted that economic development of a nation is accompanied by a ‘westernisation’ of the diet, epitomised by increased intake of meats, fats, processed foods, sugar and salt (Kearney, 2010). This so-called ‘nutritional transition’ has the effect of replacing population-level malnourishment with nutrition related non-communicable diseases (NR-NCDs) such as obesity and diabetes which predominate where increased consumption of unhealthy foods occurs (Popkin, 1999).

Increased food consumption has several diverse driving forces. Changes in income (global per capita income is projected to rise by at least 2 per cent per annum in the next 40 years, Du et al., 2004), urbanisation (mass media, improved distribution infrastructure, large supermarkets and access to foreign suppliers, Hawkes, 2006), trade liberalisation (leading to increased supply of processed foods, growing urbanisation and changes in consumer lifestyle, Thow, 2009), trans-national food corporations (particularly in the fast-food market, leading to ‘westernisation’ of lifestyles, Hawkes, 2005) and improved food retailing (e.g. leading to rapid expansion of supermarket networks, particularly in Latin America and Asia; Reardon and Swinnen, 2004), are all implied.

The development of a national economy is generally accompanied by a subsequent decline in the relative output from the agricultural sector of that nation. Accompanying this shifting output has been a significant acceleration in globalised food trading due to improvements in supply chains, international trading agreements and technology (Anderson, 2010). Changing demand for food associated with demographic alterations within increasingly large sub-populations of the globe leads to direct questions about future food supplies and to so-called global ‘food security’. Food security has been defined as the scenario whereby ‘all people, at all times, have physical, social and economic access to sufficient, safe and nutritious food to meet their dietary needs and food pref-

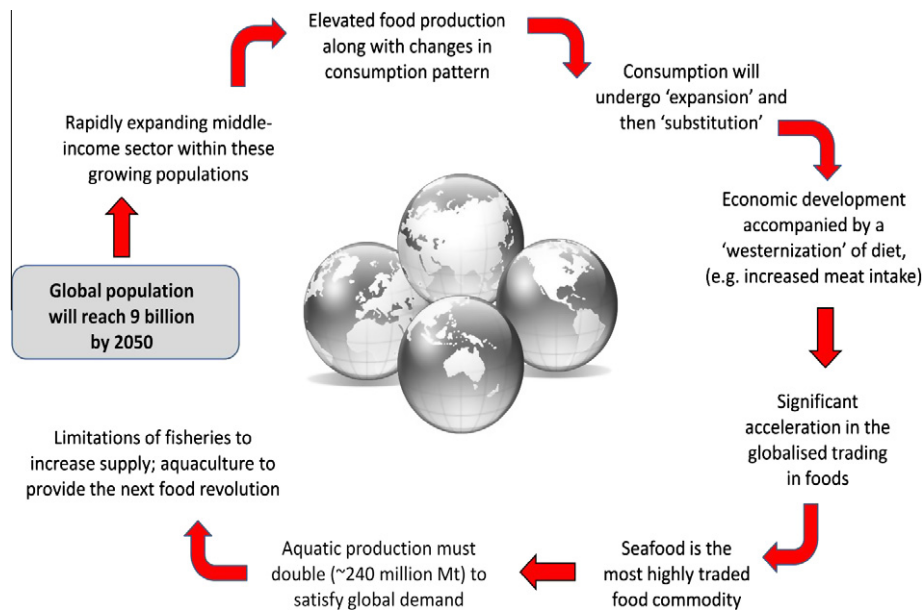


Fig. 1. Global food security and projected production demands from the aquatic food sector in context. Expansion in the global population and associated demographic shifts in particular regions lead to increased consumption of meat protein (included that from aquatic animals). Accelerated demand leads to further development of global trading pathways. Production must expand to meet increased (and diversified) demand but limitations on wild capture place strong emphasis on farming of aquatic animals.

erences for an active and healthy life' (FSN Forum 2007; <http://km.fao.org/fsn/>). In the context of this, Godfray et al. (2010) states that although globally 1 in 7 do not have sufficient access to food, a similar proportion is overfed. Furthermore, this increased demand for food must be placed into context not only with concomitant increases in competition for land, water and other resources, but also with exogenous factors such as climate change, all of which will affect how food is produced efficiently and sustainably. Global food security, particularly in light of these factors must therefore be considered an aspiration rather than a statement of reality, and one that will require significant multi-national engagement to be achieved.

In terms of animal protein, terrestrial livestock systems occupy about 30 per cent of the world's ice-free surface area (Steinfeld et al., 2006), are worth an estimated US \$1.4 trillion, and employ over 1.3bn people globally (Thornton, 2010). Global production of protein from aquatic animals includes output from marine and freshwater aquaculture (which has grown dramatically over the past 50 years to supply over 50 million Mt at a value of US \$100bn per annum; Bostock et al., 2010), and from capture fisheries which contribute 144 million Mt from marine and inland waterways (Garcia and Rosenberg, 2010). In this context, it should be recognised that aquaculture has grown faster than any other food-producing sector over this period and is projected to supply more than 50% of aquatic foodstuffs by 2015 (Bostock et al., 2010). The Asian sub-continent dominates aquaculture production (89% by volume, 79% by value), with China the largest producing nation (>32 million Mt in 2008) (Bostock et al., 2010). In terms of consumption of protein from aquatic sources (fish, shellfish etc.), the highest increases in seafood consumption have occurred in Oceania and Asia, and especially in China where consumption has increased from 11 g to 69 g per person per day over the period 1963–2003. In addition, developing nations have also markedly increased consumption of freshwater fish, with 10-fold increases in countries such as China over the same period (Kearney, 2010). By 2050, aquatic production will need to reach 231 million Mt (almost double the current production) to supply global demand (Kearney, 2010). In light of limitations of the ocean fisheries to provide increased supply over this period, aquaculture, and particularly that

derived from the marine environment, has the potential to fill the deficit and to provide the next food revolution (Duarte et al., 2009) (Fig. 1).

Although the FAO state that over 300 species are farmed in the global aquaculture industry, five species account for one third of output by volume (19% value) and ten species for over half of volume (45% by value) (FAO, 2009). Of these key species, the FAO predict that annual production of wild capture and farmed crustaceans (the focus of this review) exceeds 10 million Mt with first sale value of almost \$40bn. Fisheries contribute approximately 60% by weight and 50% by value, with aquaculture production forming the remainder. Fisheries are dominated by marine shrimp (\$12bn), crabs (\$3.7bn), lobsters (\$2.4bn) and freshwater crustaceans (\$1bn) (<http://www.fao.org>). Marine shrimp form the most significant proportion of the aquaculture sector (>3 m metric tonnes, first sale value \$12bn), with cultured freshwater crustaceans (\$4.7bn), and other miscellaneous species contributing the rest (data for 2006; <http://www.fao.org>). Whilst wild fishery production has remained largely static, aquaculture production of key species including Pacific white shrimp (*Penaeus vannamei*) have undergone rapid global expansion since 2000, ranking in the top 10 species by production quantity and number one for production value (\$9bn). Tiger shrimp (*Penaeus monodon*) adds a further \$3bn per year in production value (<http://www.fao.org>). Production of cultured crustaceans is predominantly focussed in Central and South America and Asia, particularly China. Consumption of product occurs more widely and exports are focussed on the USA, Japan and the European Union. This geographic separation of net consumers from net producers in many cases, epitomises the globalised industry for crustacean food products and highlights the status of shrimp as the most important seafood product traded internationally (Stentiford et al., 2010b). With the backdrop of global production, this review will focus specifically on the issue of food security from the wild and farmed crustacean sector, particularly with regard to the negative impact of pathogens on past and current production, international legislative frameworks with the potential to impact upon the trading of live crustaceans and their products, and potential mechanisms to mitigate the effects of disease in farmed and wild populations. More comprehensive reviews

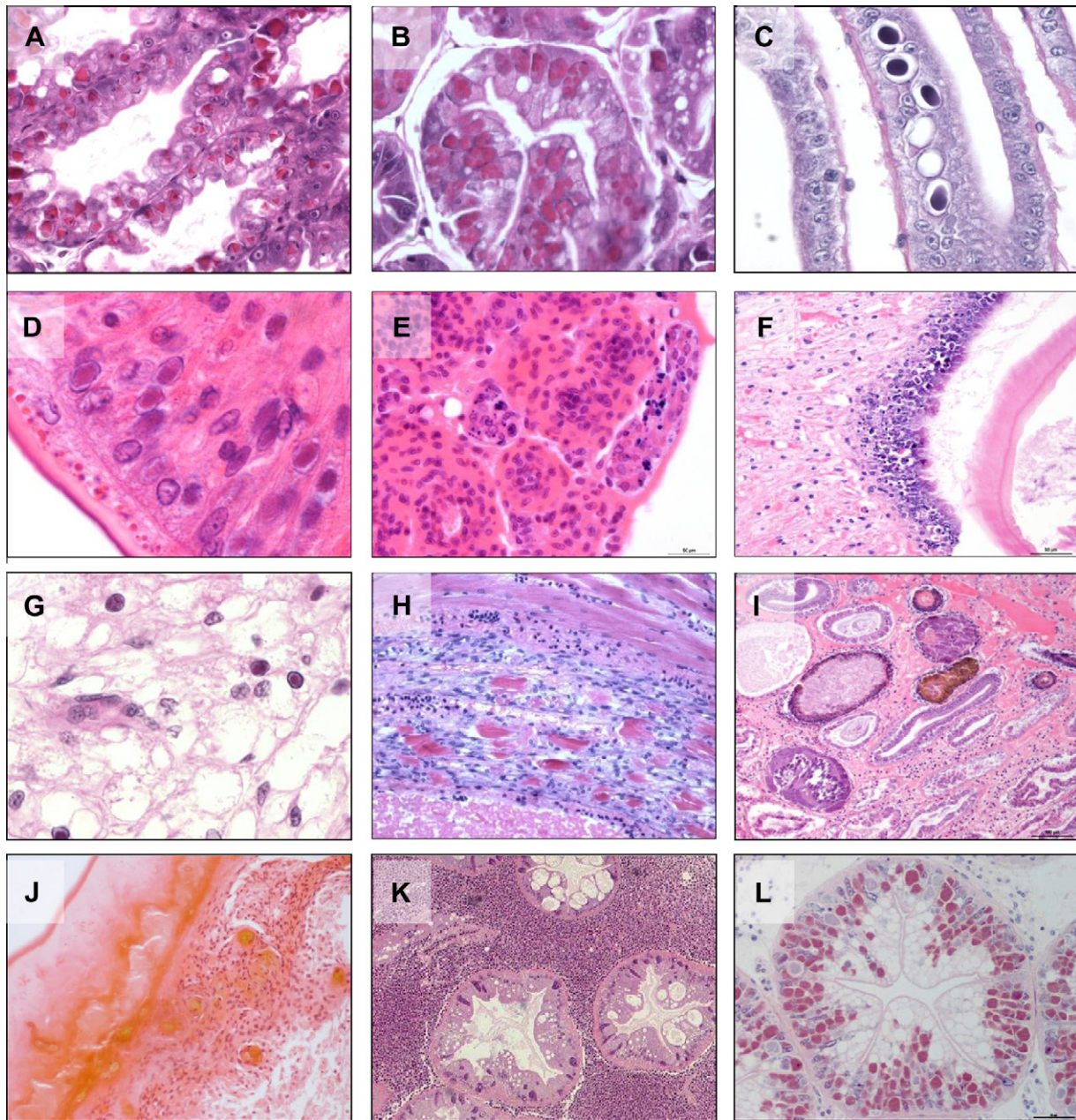


Fig. 2. Key pathogens causing negative impacts in the global crustacean aquaculture and fisheries sectors. Those marked with * are currently listed by the OIE (2012). (A) *Baculovirus penaei* (BP). (B) *Penaeus monodon* nucleopolyhedrovirus (PemoNPV) (=Monodon Baculovirus, MBV). (C) Hepatopancreatic Parvovirus (HPV). (D) White Spot Syndrome Virus (WSSV)*. (E) Taura Syndrome Virus (TSV)*. (F) Yellowhead Virus (YHV)*. (G) Infectious Hypodermal and Hematopoietic Necrosis Virus (IHHNV)*. (H) Infectious Myonecrosis Virus (IMNV)*. (I) Necrotizing Hepatopancreatitis (NHP)*. (J) Crayfish plague caused by *Aphanomyces astaci**. (K) *Hematodinium* sp. dinoflagellate parasites. (L) Microsporidian pathogens such as *Hepatospora eriocheir* (Stentiford et al., 2011).

of the specific diseases covered are available elsewhere in the literature.

2. Diseases of crustaceans

Decapod crustaceans (including crabs, shrimp, lobsters and crayfish) can play host to a wide range of pathogens and parasites (Fig. 2). Viral infections have been encountered in both wild and cultured crustaceans; since their initial discovery in this host group in the 1960's (Vago, 1966), there have been over 50 viruses described from a diverse range of crustacean groups. Due to their larger size and characteristic pathology, the DNA viruses (epitomised by the bacilliform viruses of the hepatopancreas of many crusta-

ceans, the white spot syndrome virus of penaeid shrimp, and the virus infection of spiny lobsters, PAV1) have been described in most host groups studied with any level of detail (for examples see Takahashi et al., 1994; and Stentiford, 2008; Behringer et al., 2011). Viruses with RNA genomes, some of which have devastating consequences for cultured populations, are also being increasingly described, particularly from intensively farmed penaeid shrimp hosts (for examples see Boonyaratpalin et al., 1993; Hasson et al., 1995; Poulos et al., 2006; Lightner, 2011). Whilst relatively little is known about viruses of wild crustaceans, it is critical that as much data as possible be collected on viral pathogens from wild decapod stocks (Johnson, 1984; Bonami and Lightner, 1991). Free-living bacterial infections of crustaceans are associated either with the exoskeleton (e.g. Getchell, 1989), or the haemolymph

(Tubiash et al., 1975; Wang, 2011). Intracellular bacterial infections occur within specific types of host cell (see Vincent et al., 2004; Eddy et al., 2007). Fungal pathogens (Phycomycetes, Ascomycetes and Fungi Imperfecti) have been implicated in catastrophic epidemics and mortality events in decapod crustaceans (Unestam, 1973). Egg mortalities and larval mycoses have been associated with *Lagenidium*-like fungal infections in wild crabs (Fisher and Wickham, 1975; Armstrong et al., 1976). Yeast infections co-occur with parasitic dinoflagellate infections in wild crabs (Stentiford et al., 2003) whilst introductions of *Aphanomyces astaci* has led to widespread mortalities in several European crayfish species over the past century (Longshaw, 2011). Protistan pathogens have been widely reported from crustacean hosts. A wide taxonomic spectrum of protists infect non-commercial hosts such as the shore crab *Carcinus maenas* (Stentiford and Feist, 2005) while several parasites within this group, including parasitic dinoflagellates of the genus *Hematodinium*, cause potent disease in an increasing range of commercially exploited decapod crustaceans (Stentiford and Shields, 2005; Morado, 2011; Small, 2012). Others, including representatives of the Phylum Microsporidia (protist-fungal border) are described infecting hosts across a wide range of habitat types from freshwater to marine, and cause patent disease in affected hosts. The majority of infections infect either the host musculature (e.g. Myosporidae, Stentiford et al., 2010b) or the hepatopancreas (e.g. Hepatosporidae, Stentiford et al., 2011). In some cases, microsporidium infections of crustacean hosts have been demonstrated to have close relationships with those found infecting vertebrate hosts (e.g. *Enterospora* in marine crabs, Stentiford et al., 2007, 2011), providing evidence for multi-trophic transfer between invertebrates and vertebrates. Finally, decapod crustaceans are infected by a wide variety of metazoan parasite life stages. These include worm infections by members of the Trematoda, Cestoda, Acanthocephala, Nemertea and Turbellaria, and the parasitic crustaceans of the Copepoda, Rhizocephala and Isopoda. Comprehensive surveys of metazoan parasites in wild crustaceans were carried out during the late 19th and mid 20th centuries (see Stentiford, 2008 for context) though recent interest in those with zoonotic potential, such as the oriental lung fluke (*Paragonomus westermanii*) spark occasional interest in their presence in edible crustaceans (Liu et al., 2007).

Viral pathogens appear to exert the most significant constraints on the growth and survival of crustaceans under culture conditions. However, the available literature indicates that protistan pathogens appear to elicit the greatest detrimental effect in wild crustacean hosts. These pathogens also affect the marketability of commercial products harvested from these hosts. This may reflect some artefact of the manner in which scientists approach the sampling of wild crustacean populations; in which rapidly lethal viral pathogens, for example, may go relatively undetected. Recent work focussing on the un-fished (juvenile) proportion of crustacean populations has furthermore demonstrated a significantly different pathogen profile in these cohorts when compared with adults of the same species; another potential contributor to so-called 'silent mortalities' in wild crustacean populations (Shields and Squyers, 2000; Bateman et al., 2011).

Disease research in crustacean hosts is focussed on the utilisation of a combination of traditional (e.g. histopathology, transmission electron microscopy) and modern (molecular) diagnostic approaches. As for other major animal groups, standardised protocols for the diagnosis of specific diseases of crustaceans are provided in the frequently updated *Manual of Diagnostic Tests for Aquatic Animals* published by the World Health Organisation for Animal Health (OIE, 2009). The pathogens currently listed in this manual (and therefore notifiable to the OIE) are principally virus infections of farmed penaeid shrimps, but the list is frequently reviewed to reflect emerging and persistent disease issues in farmed

and wild crustacean hosts. Whilst the lack of continuous cell lines for crustacean organs and tissues hampered fundamental research into crustacean viruses, it has encouraged histopathological and ultrastructural approaches to studying pathogenesis and pathogen identification. When combined with molecular approaches to pathogen phylogeny, these methods have provided novel insights into pathogen taxonomy based upon comparative morphological and nucleic acid data (e.g. Stentiford et al., 2010b).

3. Diseases and the food supply from crustacean aquaculture

3.1. Where do disease agents come from?

The growth of the penaeid shrimp industry stems from early research into optimising husbandry conditions for shrimp growth (mainly in Asia, between the 1930's and 1960's). This was followed by commercial up-scaling from the late 1960's and the early 1980's, and international expansion of the industry in the subsequent period to date. The penaeid aquaculture industry is now globalised, though principally confined within the tropics to the region 15° north and south of the equator (Cheshire, 2005). The large volume of published literature on the association between infectious disease agents and farmed penaeid shrimp provides compelling evidence for the major constraint that these pathogens have imposed on efficient production and yield in intensive aquaculture systems (Lightner, 1993, 2011; Flegel, 2006a). Despite difficulties in gathering accurate economic data on the effect of pathogens on crustacean production, approximately 40% of potential tropical shrimp production is estimated to be lost to infectious diseases each year (Lundin, 1996). Around 60% of current disease-associated losses in shrimp aquaculture may be due to viral pathogens with a further 20% to bacterial pathogens. By comparison, losses associated with fungal and parasitic agents are less (Flegel, 2006b, 2012). In broad terms, since the inception of the industry, production has been plagued by an increasingly cryptic array of pathogens that continue to emerge despite efforts to create specific-pathogen-free (SPF) stocks and apply improved farm management systems. Unfortunately, disease emergence and spread corresponds to poor industry practice with potential to rapidly impact whole regions. The propensity to house farmed stocks adjacent to (and in direct contact with) natural waterways (and their resident wildlife) will likely further contribute to novel disease emergence, even in originally SPF stocks of penaeid shrimp. In many such scenarios, it cannot be definitively stated whether emergent diseases are indeed original pathogens of penaeid shrimp or opportunistic invaders from the surrounding fauna. Improved siting of farms in biosecure settings will likely contribute to a reduced emergence rate of significant pathogens in penaeid shrimp (Flegel, 2012). In other scenarios, diseases have emerged in penaeid shrimp following their feeding on non-penaeid carcasses. This pathway may have been responsible for the emergence of WSSV in penaeid shrimp hosts in Asia since shrimp broodstock in hatcheries were commonly fed imported frozen crabs in the period prior to the outbreak. Morphologically similar viruses to WSSV have recently been described infecting portunid crabs in Europe (Bonami and Zhang, 2011).

The emergence and trans-boundary distribution of pathogenic agents associated with penaeid shrimp production is well documented within the existing literature, and brought up to date by reviews contained within this volume, both for the Americas (Lightner et al., 2012) and for Asia (Flegel, 2012). Prior to 1990, due to limited trans-boundary movement of aquaculture animals and their products, pathogenic agents affecting shrimp production were largely confined to specific geographic locations. For this reason, during the early industrial expansion of the industry, no

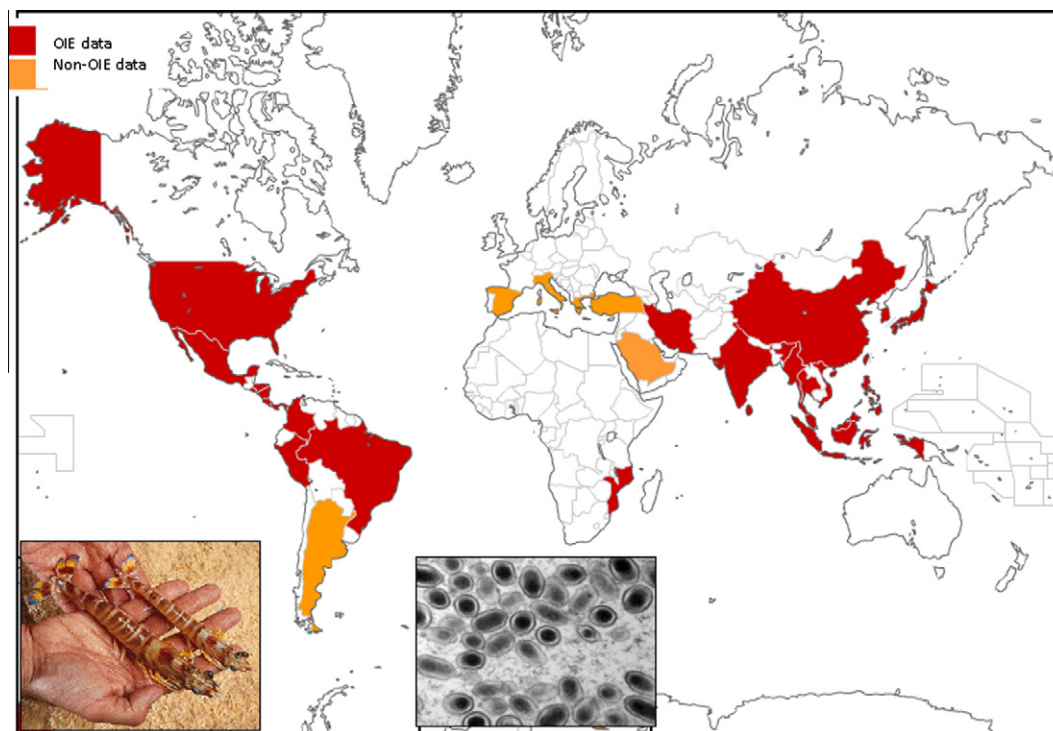


Fig. 3. Global status of nations with historic reports of White Spot Disease (WSD) caused by white spot syndrome virus (WSSV) according to OIE official notifications (red) and non-official reports (orange) at time of writing (www.oie.org). Initial outbreaks occurred in *Marsupenaeus japonicus* (Holthuis, 1980) (inset left) farmed in eastern Asia during the early 1990's. The subsequent pandemic caused by the virus (inset centre) reached Central and Southern Asia, Latin America and Southern Europe by the mid-late 1990's. Later the virus caused outbreaks in the Middle East. The first official outbreak in Africa occurred in Mozambique in 2011.

shrimp diseases were listed by the World Animal Health Organisation (OIE). Subsequent expansion of the industry, and the increasingly globalised trade in broodstock, larvae and commodity products arising from shrimp farming led to the emergence of several significant disease conditions in both the Americas (e.g. *Baculovirus penaei*, necrotizing hepatopancreatitis, Taura syndrome, infectious myonecrosis) and in Asia (spherical baculovirus, yellow-head disease, white spot disease). The majority of these diseases have caused significant production issues in shrimp farming regions distant from their original site of emergence. Furthermore, some of them are listed by the OIE, highlighting their ongoing importance as negative constraints to production and yield from the industry. In addition, they have potential to affect non-farmed populations of susceptible crustaceans (OIE, 2009; Stentiford et al., 2009, 2010a; Lightner, 2012). It is also noteworthy that since 1993, due to domestication and genetic stock selection of Pacific white leg shrimp (*P. vannamei*), that large-scale production has shifted away from the formerly dominant black tiger shrimp (*P. monodon*) (Flegel, 2012; Moss et al., 2012). Whilst domestication of stock is clearly a major step forward in terms of yield improvement and disease control at the farm and country level, it may also be argued that the concentration of the majority of global effort into production of a single species of penaeid shrimp has certainly aided the translocation of important pathogens to distant regions (e.g. infectious myonecrosis virus has been endemic in shrimp farms in Indonesia since 2006 following its emergence in Brazil in 2002). The relative naivety of domesticated stocks of *P. vannamei* to novel geographic locations may also increase the potential for disease emergence in this translocated species, particularly where farmed stock is maintained in ponds with direct contact to natural waters, and their wildlife (see above).

3.2. White spot disease – a thorn in the side of global shrimp aquaculture

White spot disease (WSD) due to infection with white spot syndrome virus (WSSV) provides the single most striking example of a pathogen negatively impacting the production of food (and wealth) from the crustacean aquaculture sector. Despite over two decades since its emergence in Asia, WSD continues to plague shrimp the major farming regions in Asia and the Americas, and to threaten new locations where shrimp farming operations are in their infancy (OIE, 2009) (Fig. 3). Using data from several sources, Lightner et al. (2012) predict that global production losses due to WSD have been at least \$8bn since its emergence in the early 1990's but also state that actual losses may be closer to \$15bn. In this context, it outweighs the impact of several other important crustacean pathogens currently listed by the OIE: IHNV (\$1bn), YHD (\$0.5bn), TSV (\$3bn) and IMNV (\$1bn). Considering the higher end production loss figure, this equates to an approximate \$1bn per annum loss to global shrimp aquaculture associated with WSD. Based upon current annual production of \$10bn, an estimated 10% of output is lost each year to WSD alone. Taken together, the top five viral pathogens (WSSV, YHV, TSV, IHNV and IMNV) may account for additional annual losses of approximately \$500 m, giving an annual loss due to the top five viral pathogens of around \$1.5bn (or 15% of production). Although figures stated are broad estimates of losses incurred due to these pathogens, it is interesting to note that although some viruses (such as IHNV) appear to cause longer term chronic losses to the industry (amounting to \$ < 50 m per annum since emergence according to figures given by Lightner et al. (2012), other pathogens, such as WSSV (\$1bn per annum), TSV (\$200 m per annum) and IMNV (\$200 m per annum) continue to

impart significant annual negative effects. If one considers the 15% production loss in terms of volume (currently estimated at >3 m metric tonnes per annum), the top five viruses prevent production of almost 500,000 metric tonnes of shrimp per annum, equivalent to the total importation of shrimp products to the European Union, or to the USA, in a year. In these terms, WSD alone accounts for volume losses amounting to 300,000 metric tonnes per annum, more than the total importation to Japan within a year (Import figures based upon 2006 in <http://www.fao.org>). Given population projections and considering maintenance of supply at the current rate, the entire aquaculture industry output would need to double in the next decade in order to keep pace with population growth (FAO, 2009). Making a presumption that penaeid shrimp continues to play a key role in this expansion, 6 m metric tonnes of production would be required by 2025. Considering current rates of production loss to WSD (10% of total) and the top five viral diseases (15% of total), a shortfall equivalent to the current imports of the whole of the USA and EU combined would be predicted. Given worst case scenarios for tropical shrimp production losses by Lundin (1996) of 40% per annum, production shortfall would equate to almost 3 m metric tonnes – the equivalent of total current global production. To this end, the World Bank report recommended investment of US\$275 million in shrimp disease research over the following 15 years (Lundin, 1996). Despite significant advances in understanding viral pathogenesis and mitigation of disease in crustaceans, it is not clear whether this level of research investment has occurred to date.

3.3. Infectious myonecrosis virus – a lesson not learned

As stated above, expansion of the global shrimp farming industry between the mid-1980's and the present day have aligned with an increasing perception of the potential for trans-boundary movement of disease agents in broodstock, larvae and commodity products; especially for pathogens included in international legislative frameworks such as that provided by the OIE (OIE, 2009) and the EU (Stentiford et al., 2010a). However, despite this seemingly increased awareness, the rapid global spread of emergent pathogens continues to occur. The emergence of Infectious Myonecrosis (IMN) caused by infectious myonecrosis virus (IMNV) in Brazil in 2003, and its subsequent spread to *P. vannamei* farms operating in Indonesia by 2006 epitomises the 'lesson not learnt' from previous experiences with illegal trading of infected broodstock (Flegel and Fagan, 2002; Flegel, 2006c; Senapin et al., 2007). The emergence and global translocation of IMNV is a particular cause for concern since it has rapidly established itself amongst the top five viral pathogens and is likely to spread further through the Americas and Asia despite its listing by the OIE in 2005 (OIE, 2006). Estimated losses due to IMN in Indonesia already amount to over \$1bn and although Flegel (2012) predicts that IMN may not spread rapidly through Asia due to awareness on risks of broodstock and larval imports (including quarantine and testing for IMNV), illegal movements cannot be ruled out and may more easily occur now that the virus has been detected outside of South America. Flegel (2012) also proposes that all Asian nations farming *P. vannamei* should implement monitoring and emergency response procedures to deal with unexpected outbreaks associated with IMNV.

3.4. What is in store?

Domestication and the production of SPF stocks have undoubtedly led to significant improvements in survival and yield, particularly when their 'high health' offspring are stocked into biosecure facilities (Moss et al., 2012). The systematic appearance of commercially damaging viral epidemics in the years preceding such initiatives is testimony to the potential for intensive stocking to

convert cryptic viral infections to emerging disease problems in captive penaeid shrimp. Maturation of the penaeid shrimp farming industry over coming years will likely lead to greater emphasis on the siting of farms in increasingly biosecure environments where physical barriers protect farmed stock from wild reservoirs, and *vice versa* (Moss et al., 2012). In this context, it is perhaps feasible that the emergence rate of novel infectious agents of penaeid shrimp will decrease to a level significantly less than that observed during the major expansive phase of the industry. Although other avenues of disease introduction are possible, including potential for industrial sabotage (see Jones, 2012), stringent control over movements of live animals and their pathogens will remain a top priority for those countries wishing to secure long term sustainability in their shrimp farming industry.

Expansion of the global crustacean aquaculture industry has not solely relied on penaeid shrimp farming. Freshwater crustaceans now contribute almost \$5bn to global trade, with species such as *Macrobrachium* spp. (300,000 metric tonnes per annum) and the freshwater crab *Eriocheir sinensis* (almost 500,000 metric tonnes per annum) being the key farmed species. Rapid expansion in culture of the latter was in direct response to an attempted diversification in the Chinese industry (www.fao.org). As for penaeid shrimp, the rapid growth in freshwater crustacean farming has been blighted by several important disease issues. *Macrobrachium rosenbergii* culture is impacted by the OIE listed *M. rosenbergii* Nodavirus (MrNV) and its associated satellite, Extra Small Virus (XSV) (Bonami and Sri Widada, 2011) which cause so-called White Tail Disease (WTD) and mass mortality in hatcheries and farms (Bonami and Sri Widada, 2011). *E. sinensis* has a number of pathogens, including a rhabdovirus causing 'Sighs Diseases' (Zhang and Bonami, 2007), and an economically devastating infection by *Spiroplasma eriocheiris* which causes 'Tremor Disease' (Wang et al., 2011). In other examples of non-penaeid crustacean culture, mud crabs (*Scylla* spp.) are the subject of a rapidly expanding industry in Asia and some parts of Africa, with production of over 138,000 metric tonnes (\$377 m) in 2008. Culture of this species has been affected by several important pathogens in recent years, including 'milky disease' associated with the parasitic dinoflagellate *Hematodinium* (Li et al., 2008). Interestingly, this is the first example of this important pathogen of wild crustaceans (see below) causing negative effects in farmed crustaceans. Furthermore, recent work has demonstrated how shrimp (*Exopalaemon carinicauda*) co-cultured with crabs (*Portunus trituberculatus* and *Scylla serrata*) in China are also susceptible to infection by *Hematodinium* sp. (Xu et al., 2010), with up to 100% mortality during outbreaks. The emergence of *Hematodinium* sp. as a problem pathogen in Chinese aquaculture is clearly a consequence of diversification into novel aquaculture species and is reminiscent of the emergence of non-viral pathogens during early attempts to culture and upscale production of penaeid shrimps (see above). The description of *Hematodinium* sp. infection in *E. carinicauda* is the first example of susceptibility to this pathogen in shrimp and likely reflects the specific stressors imposed on *E. carinicauda* under intensive culture conditions. This example shows the potential for novel pathogens to pass from species to species under polyculture conditions and the role of wild reservoirs in disease emergence in aquaculture.

Finally, freshwater crayfish farming is dominated by the production of red swamp crayfish (*Procambarus clarkii*), principally in China, the USA and Scandinavian countries. Global production exceeded 500,000 metric tonnes during 2009 with first sale values of over \$2.4bn. Although pathogenic agents have been reported from *P. clarkii*, the extensive (rather than intensive) nature of their culture has apparently averted serious disease problems (www.fao.org). The expansion of this industry in other regions is, however, somewhat limited by the vector potential of *P. clarkii* for 'crayfish plague' caused by *A. astaci* (Longshaw, 2011).

4. Disease and food supply from crustacean fisheries

4.1. Disease effects in wild stocks

The open nature of crustacean fisheries coupled with a relative lack of directed effort to survey for infectious agents and their associated diseases has led to a significant deficit in knowledge on causes of mortality in even our most commercially significant species. Dedicated field surveys have focussed on the prevalence of specific pathogens in fished populations of fisheries species such as European edible crab (*Cancer pagurus*) (Stentiford et al., 2002), Norway lobster (*Nephrops norvegicus*) (Stentiford et al., 2001), American lobster (*Homarus americanus*) (Stewart, 1975), brown shrimp (*Crangon crangon*) (Stentiford et al., 2004), spiny lobster (*Panulirus argus*) (Shields and Behringer, 2004), snow and tanner crabs (*Chionoecetes* spp.) (Meyers et al., 1996). Other efforts have attempted to gather field data relating to the prevalence and profile of pathogens over extended time periods or across different seasons in a range of commercially and ecologically significant species (e.g. Shields, 1993; Messick, 1998; Stentiford and Feist, 2005; Shields and Overstreet, 2007; Stentiford, 2008). The majority of studies to date have focussed on the presence of pathogens in the fished portion of the population (i.e. the proportion over the minimum landing size) since these animals are more convenient to sample from either fishers, or market places dealing in live animals for human consumption. Whilst these studies offer researchers an insight into the presence of pathogens in a given sub-population, bias in the survey design linked to selectivity for or against diseased animals via fishing gear, pre-selection (removal) of diseased animals by fishers, and the potential for post-capture mortality of animals with patent disease prior to sampling may all affect the survey outcome (e.g. Pestal et al., 2003). Furthermore, recent studies focussing on comparative pathogen profiles in juvenile and adult life stages of crabs (*C. pagurus*) have demonstrated a propensity for higher prevalence and a different pathogen profile in these stages sampled over a whole year (Bateman et al., 2011). Data of this type are likely to be important in understanding the potential for disease to cause 'silent mortalities' (i.e. unobserved) in commercially exploited crustacean stocks and may also be used to develop cohort-to-cohort mortality models for fisheries stock assessment (e.g. Shields and Overstreet, 2007; Bateman et al., 2011). Nevertheless, the ability to accurately assess the negative contribution of disease to wild crustacean fisheries in terms of production losses is far more challenging than similar assessments of farmed crustacean stocks (see above).

With some notable exceptions (e.g. PaV1 infection of spiny lobsters), most reported cases of disease occurring at significant prevalence in wild crustaceans relate to infection by protistan pathogens. In particular, attention in the past two decades has focussed on the *Hematodinium*-like parasitic dinoflagellates infecting a growing number of decapod crustacean species (for review see Stentiford and Shields, 2005; Small, 2012). In the majority of hosts studied to date, infection leads to a characteristic disease state in which the haemolymph is progressively invaded by vegetative and sporulative stages of the dinoflagellate. The disease has caused significant marketing issues in the industry for snow and tanner crabs (Meyers et al., 1987), and is likely responsible for the total collapse of fisheries in some regions (e.g. Wilhelm and Mialhe, 1996). It is also being reported more frequently in species and locations where presence and prevalence have been historically low (e.g. Pestal et al., 2003; Shields et al., 2007). Whether this represents an increased awareness (and therefore reporting) of *Hematodinium*, or alternatively a true increase in its occurrence in the global fishery is debatable. However, evidence from certain locations (e.g. the cold water fishery for tanner and snow crabs

off Newfoundland) do provide clear evidence for significantly increased prevalence concomitant with changing ambient conditions in recent decades (Pestal et al., 2003). As stated above, it is also significant that *Hematodinium* has emerged as an important pathogen of cultured crabs and shrimp in China in recent years (Li et al., 2008; Xu et al., 2010). As highlighted by Small et al. (2012), an improved understanding of the molecular taxonomy of *Hematodinium* in the type hosts (*C. maenas* and *Liocarcinus depurator*) and comparison to variants responsible for causing disease in other important host crustaceans will be fundamental in understanding the global epidemiology of this enigmatic parasite of wild crustaceans.

Continued focus on the pathogenic agents of wild crustaceans has an important role in improving our understanding of emergent pathogens affecting cultured stocks. Furthermore, the potential for wild crustacean populations to tolerate very high prevalences of pathogens (and their associated disease states) offers an intriguing insight into the fundamental basis for host-pathogen interaction and defensive responses in the invertebrates. In several cases, infection prevalence may reach 100% (e.g. *C. crangon* bacilliform virus in Crangonid shrimps; Stentiford et al., 2004, and *Hematodinium* sp. infection of blue crabs; Messick, 1994) without causing long term decline of the host population. Diseases of wild crustaceans may therefore hold vital clues for mitigating the negative impact of pathogens in cultured crustaceans.

4.2. Can we mitigate the effects of disease in wild crustaceans?

Pathogens form a natural component of any ecosystem. In those species of wild crustaceans that have been studied with any level of detail, some appear to naturally harbour a wide diversity of pathogens (e.g. *C. maenas*) (e.g. Stentiford and Feist, 2005) while for others, the diversity of pathogens is lower (e.g. *Homarus* spp.) (e.g. Cawthorn, 2011). Clearly such broad statements are somewhat subject of the number of published research papers associated with disease agents in specific host taxa (often governed by their availability, ease of working with, and the financial cost of purchasing live samples), but broad experience on working with a range of decapod hosts in our laboratories seems to reflect this differential pathogen burden. For populations of some host taxa, single pathogens appear to dominate the profile (e.g. *Hematodinium* sp. in *N. norvegicus*; Stentiford and Neil, 2011) while for others, including the aforementioned *C. maenas*, and the European edible crab (*C. pagurus*), a wide range of pathogens may be encountered, with certain ones occurring at high prevalence (>50%), and others at lower prevalence (<5%) (Bateman et al., 2011). It is an oversimplification however to consider that pathogens with lower observed prevalence may be less damaging to wild populations than those occurring at higher prevalence. Cases of up to 100% prevalence of CcBV infection in Crangonid shrimps (Stentiford et al., 2004) may be less damaging for instance than a highly pathogenic viral infection such as PAV1 in *P. argus* (Shields and Behringer, 2004) which is detected at lower point prevalence in wild populations, but likely leads to death of juvenile hosts (Behringer, 2012).

Several authors have considered the potential for anthropogenic activities to alter the prevalence and outcome of pathogen infections of wild crustaceans. For example, in a review considering disease issues in the blue crab (*Callinectes sapidus*), Shields (2003) states that in addition to direct mortality, indirect mortalities may also occur whereby infected animals are somehow less able to cope with exposure to other ambient stressors, or that fecundity is reduced in diseased animals. He also highlights the problem facing those investigating disease in wild populations of crustaceans when attempting to convince resource managers that disease af-

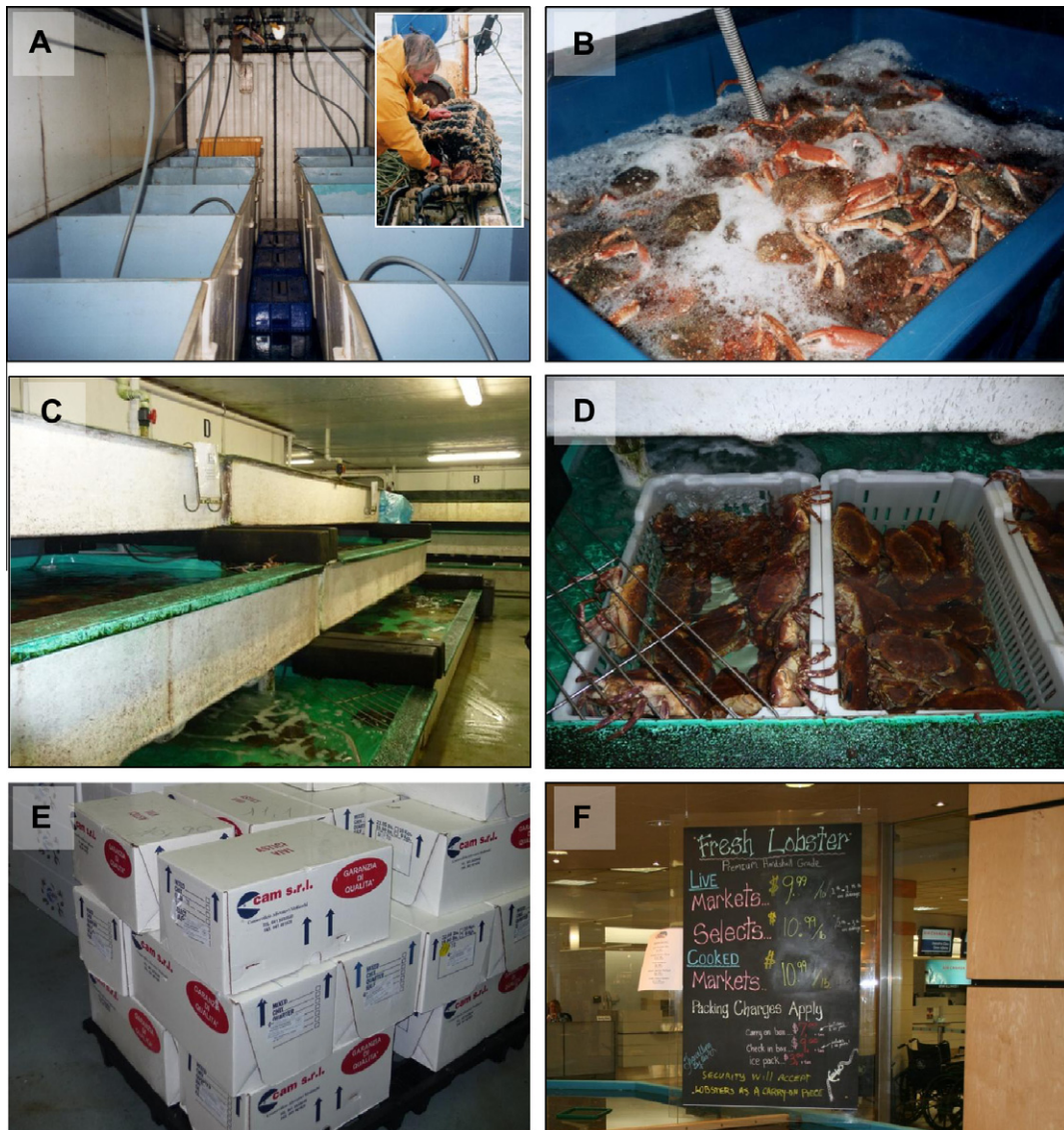


Fig. 4. The chain of custody for wild crustaceans supplied to the live market. (A) Following capture and landing by fishers (inset), live crustaceans can be transported in water to market via road. (B) Typical 'live well' in a truck transporting live crustaceans (*Maia squinado*) from the UK to continental Europe. (C). Live animals are retained prior to market in holding facilities, near market, within the recipient country (D) European edible crabs (*Cancer pagurus*) in a live holding facility in continental Europe. (E). New markets (e.g. to Asia and Europe from Canada and the USA) can be serviced by airfreight of live animals in water-free containers, directly to holding facilities within recipient countries, or even directly to consumers via sale in airport lounges (F).

fects fisheries yield. In this context, the role of disease as a contributory factor to mortality may far exceed the standard contribution of 20% as proposed in the majority of fisheries stock assessment models.

In terms of mitigating the negative impact of disease in wild populations of crustaceans, simple approaches such as the landing (and destroying) of patently diseased animals, the reduction of landing restrictions in epizootic years, overfishing of affected regions or the specific targeting of certain sexes (in which disease prevalence is highest) have all been proposed (Kuris and Lafferty, 1992; Shields, 2003, 2012). Murray (2004) used a classical epidemiological model to examine how harvesting strategy may influence the impact of an epidemic spreading as a spatial wave through a wild fish population. The impact of pre-epidemic harvesting depends on the nature of the disease. If a significant fraction of the post-epidemic population would have consisted of fish which were never infected, the post-epidemic population can be enhanced by pre-epidemic harvesting. However, as also noted by Shields (2003), we still lack fundamental knowledge on key as-

pects of the life history of important pathogens (such as the disease status of the post-epidemic population and transmission route of *Hematodinium* sp.) and importantly, on the mortality associated with certain agents. Relatively long term monitoring of crustacean populations has occurred for some important pathogens (e.g. *Hematodinium* sp. in Scottish populations of *N. norvegicus*; Stentiford et al., 2001) and in such instances, there is evidence that fishing pressure is likely to have altered the stock structure to be more conducive to epidemics (i.e. larger proportions of small, simultaneously moulting lobsters). In many exploited populations harvesting accounts for a large fraction of mortality. If fishing take is at or close to maximum sustainable yield there is no spare capacity to absorb losses due to disease outbreaks. An improved understanding of the role of fishing activity on stock structure (and disease prevalence) may therefore be utilised to avert future epidemics by altering fishing patterns in defined regions. Such approaches require closer collaboration and aligned field sampling programmes by fisheries biologists and disease researchers.

4.3. Losses associated with disease in the post-capture phase

In contrast to many other wild capture species, a significant proportion of crustaceans captured by fishers is transported live to market for subsequent human consumption (Fig. 4). In some nations (e.g. Portugal), the live trade in marine crustaceans from other European nations contributes the majority proportion of national sales. The trade itself involves a complex chain of fishers, road transportation and holding facilities which precede purchase and consumption of live products (Barrento et al., 2008). In other scenarios, live animals are shipped to distant markets via road and air following prolonged holding in the post-capture phase. In such instances, animals are often retained until market conditions are favourable (in some cases >6 months after initial capture), a particular strategy adopted by the globalised American and Canadian lobster industries, now worth over \$1bn, with annual landings approaching 100,000 tonnes (see Cawthorn, 2011; Fotedar and Evans, 2011). The live market chain is however fraught with potential stressors (poor initial selection of animals, air exposure, hypoxia, handling and physico-chemical disturbances), all of which may impact upon delivery of high quality animals to market. To this end, losses of up to 66% have been reported for live holding facilities for decapod crustaceans (for context see Barrento et al., 2008). As a result, annual losses in this phase contribute significantly to the unsustainable exploitation of wild stocks and have significant impact on future food security via this market route. To this end, several workers have highlighted the critical stages in the market chain which contribute to elevated mortality and have proposed mechanisms to reduce post-capture losses (and thereby improve animal welfare) associated with this trade (for review see Fotedar and Evans, 2011).

Several important diseases have been reported to occur in crustaceans, specifically within the post-capture phase. Gaffkemia (caused by the bacteria *Aerococcus viridans*) and so-called 'Bumper Car Disease' (caused by the ciliate *Anophryoides haemophila*) occur during the post-capture storage of *H. americanus* and are at least partly responsible for the 10–15% losses occurring annually in this industry (Lavallée et al., 2001; Cawthorn, 2011). Other infectious agents causing problems in the post-capture phase include *Hematodinium* sp. in Scottish *N. norvegicus* which has had direct negative impacts on the post-capture transportation of live animals to market, and has led to altered post-mortem degradation and earlier organoleptic rejection of product (Neil, 2012). Non-infectious conditions have also significantly affected the live trade in *N. norvegicus* – the cumulative effects of capture, emersion, handling and poor post-capture holding conditions causing so-called Idiopathic Muscle Necrosis (IMN) in a potentially large proportion of the catch (Stentiford and Neil, 2000; Ridgway et al., 2006, 2007). It is clear that the current practice of live post-capture storage of crustaceans is generally deemed a high-risk sector of the market and one that leads to significant mortalities and lower prices being paid for live commodity to fishers. In some regions (such as Europe), this has led to severe depressions in the unit price of live animals, which when combined with limited landing restrictions for certain species (e.g. *C. pagurus*), has formed a quantity, rather than quality fishery. Whether this practice is considered sustainable alongside increasing pressure on invertebrate fisheries resources is open to debate.

5. Managing and mitigating the problems

5.1. A shared responsibility between producer and consumer nations

The diagnosis of emerging disease issues and the rapid enforcement of biosecurity measures to avert the subsequent spread of pathogens are central to the prevention of regional or international

epidemics in crustacean aquaculture. In this context, an efficient National Veterinary Service is central to the global 'public good' represented by animal health systems. Although inherent within the protocols and manifestos of organisations such as the OIE (OIE, 2009; Lightner, 2012), and written into the international legislation of some regions such as the EU (Stentiford et al., 2010a; Peeler, 2012), important emergent pathogens (most recently, IMNV) continue to rapidly disseminate around the globe via existing trade pathways. The OIE is recognised by the World Trade Organisation (under the Agreement on the Application of Sanitary and Phytosanitary Measures; the SPS Agreement) as the reference organisation for setting of international standards dealing with animal health and zoonoses (see Oidtmann et al., 2011 for context). In terms of aquatic animal health, the OIE Aquatic Animal Health Code aims to assure the sanitary safety of international trade in aquatic animals (amphibians, fish, crustaceans and molluscs) and their products. This provides health measures to be used by Competent Authorities of importing and exporting countries to prevent the transfer of agents pathogenic for aquatic animals or humans, while avoiding unjustified sanitary barriers (Oidtmann et al., 2011). In 2011, the OIE had 178 member countries. The OIE International Database on Aquatic Animal Diseases (IDAAD) hosted by the OIE Collaborating Centre for Information on Aquatic Animal Diseases (<http://www.cefas.defra.gov.uk/idaad/>) publishes data on the occurrence of the OIE-listed aquatic animal diseases (including those of crustaceans) in all member countries. The data are grouped into 'OIE data' (official notifications by member countries to the OIE) and 'non-OIE data' (non-official data for a specific country, published in the scientific literature). It is interesting to note that for specific crustacean diseases (e.g. WSD) official notifications (28 countries in five host species under natural occurrence) is significantly short of the 40 countries in 42 host species under natural occurrence when 'OIE data' and 'non OIE data' is taken together (see Fig. 3). This reflects the considerable under-reporting of notifiable diseases to the OIE by member country Competent Authorities (Lightner, 2012). The cause of this under-reporting has several potential causes. In some cases it is due to a lack of expertise with regard aquatic animal diseases within the Veterinary Services of the member country (Lightner, 2012). In other cases, it may reflect the politics surrounding the reporting of such diseases with regard to the perceived effect that such reporting may have on the international trading of animals and their products. Another case may be the lack of resources available for testing and controlling for these diseases.

Increasing focus on the control of trans-boundary movements of crustacean pathogens is also reflected in recent changes in regional legislation. Within the EU, Council Directive 2006/88/EC adopted during 2008 has introduced controls for crustacean disease at the European level for the first time. It lists three crustacean diseases (WSD, YHD and TS) in recognition of their global importance in causing significant economic losses and the potential for their international transfer via transboundary trading in live animals and their products (Stentiford et al., 2010a). Whilst movements of live aquatic animals offers the most efficient means for global distribution of pathogens, studies have also demonstrated the potential for introduction of novel hosts in new geographic regions via trading in aquatic animal products, particularly where climatic regimens in receiving countries are suitable for pathogen survival and replication (Durand et al., 2000, 2003; Reville et al., 2005; Hasson et al., 2006; Bateman et al., 2012; Jones, 2012). Taken together, the expansion of crustacean aquaculture into new regions, the wide host susceptibility range to certain pathogens (such as WSSV) and the significant international trade in raw, frozen commodity products have lead to a wider appreciation of the negative impacts of (in particular) penaeid shrimp pathogens, in temperate regions. Based upon the fact that such regions (EU, USA,

Japan) are also the primary markets for these products, it is clear that future efforts for minimising the negative impact of disease is not only directed at those countries in which culture industries are based but also where products are destined. A central issue for health-related global public goods is how best to ensure that such collective action for health is indeed taken at the global level. Furthermore, investment into disease mitigation strategies that promote a sustainable food supply from the aquatic sector is a responsibility of both governments and those appropriate industries in net producing and net consuming nations.

5.2. Improving knowledge on pathogens and their spread

The wide range of aquatic animals in culture combined with important anthropogenic drivers (such as the long-distance movement of live animals and their products and certain farming practices) have been implicated in the relatively high rate of disease emergence in aquatic animals compared to those farmed on land (Peeler and Feist, 2011). Although the initial source of an emergent pathogen (and its associated disease state) is often not well documented, it can be assumed that they arise either from a change in the virulence of endemic pathogens, an altered ambient status which permits patent disease to occur, or from transmission to new hosts via close contact between populations of the same or different species in adjacent wild and culture settings. Enhanced disease surveillance and monitoring of wild crustacean stocks continues to demonstrate the expansive profile of pathogens infecting decapod crustaceans (see above) but to date, few of these surveys have included wild species residing in habitats adjacent to aquaculture sites. Surveys of this type provide an inventory of endemic pathogens occurring in hosts from natural habitats and may therefore be utilised to assess the potential risk of transfer of pathogens to cultured hosts. In lieu of novel pathogen emergence in cultured hosts, the inventory may also be used to document the potential first occurrence and act as a mechanism to limit its dispersal to new sites. An understanding of the pathogens inherent within these systems is however only one part of the equation. Several recent commentaries on the potential for disease outbreaks in open ocean systems have questioned whether we are experiencing an increased emergence rate concomitant with various environmental forcing factors such as climate change or anthropogenic pollution (Lafferty et al., 2004), or whether the emergence simply reflects increased observation and our relative lack of understanding of pathogen diversity (e.g. see Suttle, 2007). In light of such reviews, it will be increasingly important to consider diseases caused by pathogens as an outcome of the interaction of host, pathogen and environment rather than simply the inherent virulence of a given pathogen *per se*. Such evidence is already well understood in certain aquaculture scenarios where high prevalence of a given pathogenic agent does not necessarily equate to disease and mortality in infected hosts; rather that environmental forcing factors alter the potential of the host to limit pathogen replication (see Walker et al., 2011 for example). It is evident therefore that understanding the potential for 'disease' rather than just 'infection' will be instrumental when assessing the risk associated with emergence of novel pathogens or further spread of those already known. In addition to natural and anthropogenic forcing factors, for crustaceans, the potential for development of disease is also strongly associated with basic features of host life history such as moult status, condition, sex and age (for example, see Bateman et al., 2011).

5.3. Harnessing the natural disease mitigation strategies of crustaceans

Certain crustacean hosts appear to naturally harbour a wide diversity of pathogens while for others, the diversity of pathogens

is considerably less (see Section 4.2). Furthermore, of those pathogens encountered, some occur at relatively low (<5%) prevalence while others may be present in almost every individual sampled from a natural population. As previously stated, this observed variation in profile and prevalence may be influenced by vagaries in sampling design, or even the level of historic effort afforded to certain species. However, broadly speaking, at least part of this variation is based upon an inherent differential ability for specific pathogens to transmit, infect, replicate, cause disease, and mortality in specific host taxa. While numerous examples exist of this differential ability in the literature, a comparison of host susceptibility to the viral pathogens WSSV (many taxa across the Order Decapoda), and TSV or YHV (generally considered more specific to certain taxa) demonstrates a clearly different host-pathogen interface in these examples (Stentiford et al., 2009). To complicate matters further, recent studies on pathogen profile and prevalence in juvenile and adults of the same species of crab (*C. pagurus*) demonstrate how susceptibility to infection and disease alter throughout the lifetime of a given species (see Bateman et al., 2011). Broadly speaking, defensive responses by a host are therefore in part governed by inherited factors (which defines 'species-level susceptibility') and by more subtle mechanisms developed during the lifetime of the host (defining 'life-stage susceptibility'). As discussed above, the latter may be further affected by environmental factors which in some create sub-optimal physiological conditions for the species and life stage in question. Taken together, the interaction of pathogens with wild crustaceans from across this natural spectrum likely holds fundamental clues for ways to mitigate disease in aquaculture. For example, studies of relatively resistant host species or life stages (e.g. to key pathogens such as WSSV) may offer more fruitful avenues of research than studying those species (and life stages) for which natural resistance to viral replication and development of disease are negligible.

Hauton (2012) reviews potential approaches to the manipulation of the host immune response for the purpose of prophylaxis in aquaculture. He states that to date, efforts have largely centred on the delivery of various pathogen associated molecular patterns (PAMPs) and the successive measurement of various immune effectors (e.g. proPO) at the gene or protein levels. However, he also states that these approaches are considered somewhat crude and likely impose a net energetic cost to the host (see also Smith et al., 2003; Christensen et al., 2005; Hauton et al., 2007). Hauton (2012) therefore states that in an aquaculture setting, '(that this)...-blunt approach cannot serve as a global solution to the problems of commercially significant diseases'. As such, effective disease therapies can only be developed through a detailed understanding of the molecular pathways involved in immune surveillance within these hosts. In this respect, observations of pathogen handling in wild populations may be utilised to identify markers of immune performance that could have direct relevance for application to farming situations. Hauton (2012) summarises by identifying five potential avenues for research development: (1) Investigations into the diversity of potential immune receptors and regulatory pathways (such as DSCAM). (2) Studies on the broad spectrum of antimicrobial peptides produced by crustaceans. (3) Understanding the basis for haemocyte proliferation *in vitro*. (4) Understanding the role of the gut in subsequent immunity and disease states; and finally. (5) Molecular studies of host-pathogen interaction (epitomised by recent advances with viral interference and RNAi strategies).

Specifically for the latter example, in their paper, Bartholomay et al. (2012) have demonstrated that augmentation of the RNA interference (RNAi) response in shrimp to suppress virus infection and associated disease is a promising, emerging approach to shrimp virus disease control. Here, short fragments of RNA recog-



Fig. 5. Typical mangrove-based shrimp farm for *Penaeus vannamei* in Latin America. (A and B) post larval rearing prior to stocking of open air ponds. (C) grow-out period in open air ponds separated from each other and from the surrounding mangrove by levees. (D and E) health assessments occur at regular intervals during the growout phase (typically lasting approximately 120 days to produce shrimp of up to 20 g). (F). Ponds are drained following harvest and may be left for a fallow period prior to re-stocking. Two or even three crops may be possible in a single year.

nise and bind complimentary dsRNA sequences, thereby preventing specific gene expression (e.g. in a virus) in a sequence-specific manner. It is thereby envisaged that natural RNAi pathways play a critical role in the arthropod innate immune response to virus infection and therefore offer significant potential for development into prophylactics for use in aquaculture (Bartholomay et al., 2012). Significant challenges do however exist in the fundamental understanding of molecular responses to viral challenge, the propensity for high-prevalence/low-disease conditions in shrimp farms, the simultaneous occurrence of multiple viral infections (and strains) within individual hosts and pond populations and significantly, the ability to deliver any potential therapeutic in an effective vehicle that offers long term protection during the grow out phase. These are all areas requiring considerable intellectual focus in coming years.

5.4. Improving husbandry and farm management

In contrast to approximately 35 species of bird and mammal that have been domesticated for use in global agriculture and food production (FAO, 2007), an estimated 300 species are farmed

in the global aquaculture industry, and many more are subjected to capture fisheries (FAO, 2009). However, in terms of crustacean aquaculture, truly domesticated species (with continuous controlled reproduction independent from input of wild stock) are somewhat limited, with an almost total global reliance on a handful of penaeid shrimp species with relatively short domestication histories. Of these, two species *P. vannamei* and *P. monodon* support the majority of the \$12bn per annum global industry (Fig. 5). Early operations with penaeids utilised wild captured broodstock to produce offspring, or even direct stocking of ponds with larvae collected from nursery habitats in coastal margins of tropical zones. Whilst important in gaining early ground in the movement of penaeid shrimp to a globally traded commodity, this practice was almost certainly responsible for significant losses due to disease during this initial period (see Moss et al., 2012). The use of wild stocks has now generally been superseded by a reliance on domesticated penaeid shrimp lines, often possessing beneficial traits for commercial rearing (such as SPF classification for key viral pathogens). It is without doubt that this transition has been largely responsible for the massive growth in global yield from this sector in recent decades (Moss et al., 2012; Lightner et al.,



Fig. 6. Commodity products traded to the European Union from the global crustacean aquaculture sector. (A) Whole, frozen raw tiger shrimp (*Penaeus monodon*). (B) Whole raw, unfrozen whiteleg shrimp (*Penaeus vannamei*). (C) Whole, ice packed portunid crabs (species unknown). (D) Frozen *en bloc*, raw tails of *P. vannamei* sold in the wholesale market. Individual Quick Frozen (IQF) tails are more commonly sold in the supermarket retail sector.

2012). In his review, Moss et al. (2012) lists the use of SPF shrimp, improvements in selective breeding, and the adoption of strict on-farm biosecurity practices as key requirements for future expansion and long term sustainability of the global shrimp industry.

In relation to mitigating the negative impact of disease, Moss et al. (2012) also highlight that although SPF lines are free from specifically listed pathogens (often those listed by the OIE), they should not be considered 'pathogen free' (e.g. it is difficult to exclude *Vibrio* spp. associations from SPF shrimp lines), nor innately resistant to those listed pathogens (even though in some circumstances, resistance traits may be bred into shrimp lines through selective breeding). Due to these inherent features, an integrated approach to on-farm biosecurity is required even when ponds are stocked with high health fry that originate from SPF stocks and may also be disease which maximise the potential for successful grow-out. Moss et al. (2012) state the role of influent water as the most significant pathway of pathogen entry into the farm system (a particular issue where farms are sited close the coast). More recent attempts to intensively farm shrimp with zero water exchange (that also exclude crustacean pathogen vectors via screens and water treatment) is the so-called Biofloc technology (BFT) that has successfully yielded crops of up to 20 metric tonnes per hectare (Taw, 2010). Moss et al. (2012) summarise by proposing that an increased focus on integrated management practices (e.g. stocking of high health fry originating from SPF shrimp stocking into BFT farms) allows breeders to focus selection pressures on growth and growout survival, rather than disease resistance, and this may lead to increased production and profitability for the farmer. Isolating the farm system in this manner is likely to have direct benefit by limiting pathogen spread from farmed to wild stocks.

5.5. Defining the risk of disease translocation in commodity products

As described in the forgoing text, the global trading of shrimp products is well established, with up to 60% of all commercially harvested shrimp being placed on the world market (Anderson, 2010; Gillett, 2008; Walker and Winton, 2010) (Fig. 6). Given the apparent high propensity for viral infections to occur in penaeid shrimp, and the documented survival of such viruses within raw frozen commodity products (Nunan et al., 1998; Durand et al., 2000; McColl et al., 2004; Reddy et al., 2011), the specific risks associated with the trading of raw product is being afforded increased attention (Stentiford et al., 2010a). In his review, Jones (2012) provides a synopsis of current opinions on the topic. Here, it is stated that the international movement of animals and their products is governed by the General Agreement on Tariffs and Trade (GATT), and the associated Sanitary and Phytosanitary Measures (SPS Agreement) of the World Trade Organisation (WTO). Responsibility for the technical issues associated with application of the SPS agreement are then vested in the World Organisation for Animal Health (OIE). Jones (2012) describes several instances where the translocation of important viral pathogens to new locations was not due to the movement of live animals. These include the outbreak of WSSV in Darwin, Australia in 2000 (East et al., 2004) and the outbreak of WSSV in Louisiana crawfish ponds in 2009 (Baumgartner et al., 2009). Furthermore, he states that in addition to the direct use of raw frozen products as aquarium/farm animal feeds, other potential pathways of introduction include discarded waste from crustacean processing plants, the use of commodity shrimp as angling baits, or even by industrial sabotage. Of these, the use of shrimp as angling baits via the diversion of product packaged for human consumption was identified as a common practice in the Import Risk Assessment carried out in Australia.

lia (Biosecurity Australia, 2009). However, Jones (2012) recognises that even in the event of pathogen introduction via this (or similar) means, the probability of establishment of infection in a naïve susceptible host is not easy to predict. Furthermore, calculation of likelihood of passage of an established infection to other susceptible hosts within the population or an ecosystem is harder still. To this end, it was noted that even though WSSV was discovered in the Darwin aquarium facility in Australia in 2000 and the initial surveys of wild crustaceans at the facility outlet also tested positive for WSSV by PCR at the time, subsequent testing of animals at the site returned a negative result (East et al., 2004). Taken together, such evidence, and that arising from several other laboratory studies, appears to demonstrate that a pathogen with a wide host range (such as WSSV) present within commodity product can be passaged to naïve hosts via normal use pathways (feeding). However, the likelihood for establishment of infection at the individual or population level, and importantly, the consequence of establishment for naïve wild populations, is not fully understood (Flegel, 2009). In addition, the likelihood of transmission and establishment appears to be further diminished in the case of relatively host specific pathogens (such as YHV) (Sritunyalucksana et al., 2010).

In spite of concern over the OIE listed pathogens, Jones (2012) argues convincingly that in numerous cases (particularly as experienced for molluscan pathogens), by the time “epidemiological significance” of a non-listed novel pathogen is recognised (a requirement by the OIE for notification of a non-listed pathogen according to Article 1.1.3.5 of the Aquatic Animal Code), the pathogen may have since spread to distant locations at which its potential effect may be more devastating than estimated from the initial description. However, countries can take measures against diseases which are not listed, and the OIE can list ‘emerging diseases’ for which the criteria of ‘epidemiological significance’ are not required. As a result, in addition to the clear legislative measures which aim to control the movement of live animals for use in aquaculture (e.g. see Stentiford et al., 2010a), any other measure to reduce the risk of translocating known or unknown pathogens via the trading of commodity products, without forming significant barriers to trade, should be welcomed. These include various Codes of Practice, packaging of products to avoid their diversion to high risk activities (such as angling), public education (via labelling and other routes) and end-user regulations such as prohibitions on use as bait (Jones, 2012). Since the majority of these measures are likely to occur post-importation, they will become the primary responsibility of importing nations. In the likely event that these additional measures entail added costs of importation, increased demand for commodity products arising from low-disease risk operators (or countries) is likely to become *de rigueur* (Stentiford et al., 2010a). In essence, as raised in Section 5.1, the responsibility for control of transboundary disease spread will increasingly be shared by producer and consumer nations.

5.6. Learning lessons

The increased perception of risk for the trans-boundary movement of pathogens in broodstock, larvae and commodity products via the inclusion of such pathogens within international legislative frameworks of the OIE and other bodies (such as the EU) is a vital tool for reducing the effects of these pathogens on global aquaculture and fisheries production. In addition, FAO initiated regional programmes, such as the ‘Better Management Practices’ approach of the Network of Aquaculture Centres in the Asia-Pacific (NACA) bring pragmatic training to the industry and have a clear role to play in increasing awareness of issues such as disease for farm productivity, profit, and ultimately the marketability of aquaculture products to foreign markets. The NACA programme also recognises

the role of sustainable aquaculture in developing rural communities via capacity building, education, training and collaboration (www.enaca.org). It is encouraging to note similar FAO-led activities to establish a ‘Network of Aquaculture of the Americas’ (<http://www.racua.org>) and the ‘Aquaculture Network for Africa’ (ANAF) (www.anafaquaculture.org). The latter initiative, which provides a virtual linkage between 10 African nations, is timely given that Africa, which currently contributes just over 1% of global aquaculture production, clearly offers significant future potential for expansion. (www.fao.org). In this context, ANAF aims to promote the development of the African aquaculture sector at national and regional levels and to do so in a sustainable manner. The recent outbreak of WSD in penaeid shrimp farming operations in Mozambique (the first outbreak of this disease in Africa) sends a clear warning of the potential for this expanding industry to be impacted by the known listed pathogens (www.oie.org). Furthermore, the farming of shrimp (and other species) in new locations, entails significant risks for emergence of novel diseases from the rich pathogen biodiversity that resides in the natural waterways of those areas. Like NACA, regional initiatives in other regions must work alongside trans-global legislative instruments to ensure that aquaculture animals reach the end of the production cycle and that traded commodity is as safe as possible with regards pathogen status.

6. Conclusions and policy implications

The Organisation for Economic Co-operation and Development (OECD) has a primary mission to promote policies that will improve the economic and social well-being of people around the world. In this context, the topics discussed in this review provide a clear statement that despite a recent dramatic expansive phase in global crustacean aquaculture production, and the ongoing, widespread exploitation of natural stocks of crustaceans from the global fishery, sustainable food production from the sector will require careful attention to the current and future issues which will limit production. Furthermore, in light of a rapidly changing global socio-economy, demand for products arising from these sectors will increase. Although not a stand-alone topic, the issue of disease mitigation is central to the delivery of increased yield from the sector. The success of aquaculture and fisheries products reaching the market place will therefore become a key concern for both net-producing, and net-consuming nations.

In the recent OECD-funded symposium on ‘Disease in aquatic crustaceans: problems and solutions for global food security’ key topics relating to current and future disease issues facing the sector were discussed. The detail of these discussions is broadly represented in the papers that follow from this review but are briefly summarised below:

Losses in farmed crustaceans are mainly associated with viral pathogens for which standard preventative measures (such as vaccination) are not currently feasible. In light of this problem, new approaches to enhancing yield including improvements in broodstock and larval sourcing, outreach to farmers for promotion of best management practices, and cutting-edge research that aims to harness the natural abilities of invertebrates to mitigate assault from pathogens (e.g. the use of RNA interference therapeutics), are urgently required. In terms of fisheries losses associated with disease, key issues are centred on mortality and quality degradation in the post-capture phase, largely due to poor grading and handling by fishers and the industry chain. Occurrence of disease in wild crustaceans is also widely reported, with some indications that climatic changes may be increasing the susceptibility of exploited species to important pathogens (e.g. the parasite *Hematodinium*). However, despite improvements in field and laboratory diagnos-

tics, defining population-level effects of disease in these fisheries remains elusive. Coordination of disease specialists with fisheries scientists will be required to understand current and future impacts of existing and emergent diseases on wild stocks.

Overall, the increasing demand for crustacean seafood in light of a high emergence rate of novel diseases, a limited ability to mitigate the disease process in farmed animals, poor post-harvest handling of wild animals, and an increasing legislative burden on the trading of live animals and their products, signals a clear warning for the future sustainability of this industry. The linking together of global experts in the culture, capture and trading of crustaceans with pathologists, epidemiologists, ecologists, therapeutics specialists and policy makers in the field of food security will allow these bottlenecks to be better identified and addressed.

Key policy-related outcomes are:

1. An increased focus is required on effective therapeutics for invertebrate pathogens and specifically those disease-causing agents affecting food production from aquaculture. Research effort is required not only in those countries where production occurs but also in those countries where consumption is centred. Trans-national research programmes, including those funded by government which promote the 'public good' arising from aquaculture should aim to combine appropriate scientific expertise with practical approaches to aquatic animal production in the field.
2. An increased focus is required on the production of domesticated crustacean lineages that possess SPF or resistance traits that provide positive benefit for food production. Increasing diversity of high-volume farmed crustacean species (e.g. in China) places a specific emphasis on development of domesticated sources for production, particularly in light of a poorly described pathogen fauna for these hosts. Furthermore, increased focus on Best Management Practice (to encompass strong biosecurity principles) and novel approaches to high-volume production (e.g. Biofloc systems) require dedicated research effort.
3. An increased focus is required on the significant wastage inherent in supply chains for live crustaceans arising from the global fishery. In some regions (e.g. EU, Canada, USA), live movement to market represents a significant proportion of total trade. Losses due to poor grading, handling, storage and transport have led to a quantity-based fishery rather than quality-based industry. Spiralling lower prices arising from trading in this high-risk product have led to systematic over-exploitation (often in fisheries for which no quota exists).
4. An increased focus on rapid response to known and emerging disease outbreaks is required. Action is needed at all levels of the stakeholder chain (from producers through to national government Competent Authorities) to ensure that appropriate measures are taken to avert the introduction of pathogens, or in case of their emergence, to report and mitigate rapidly. Effective trans-national legislative tools exist but are often slow to act, leading to rapid dissemination of the pathogen of concern. Shared responsibility programmes should emerge whereby producer nations aim to supply low disease status commodity and consumer nations introduce appropriate post-import controls to prevent live animals and their products coming into contact with local wildlife or farmed stock.
5. An Improved understanding of the pathogen-induced diseases of wild crustaceans, the role of industrial practices in expression of these diseases and further, the interaction between wild and farmed stocks (wild pathogens being the likely source of future issues in culture) is required. The latter will be particularly important in those regions where aquaculture expansion is expected (e.g. Africa). These will all require the training of spe-

cialists in crustacean disease diagnosis and control at the farm level and the specific development of expertise at a national level, particularly in those countries with significant industries. In other areas, a regional focus of expertise should be developed to allow for rapid diagnosis, control and reporting of emergent disease issues.

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